Nest survival and predation in Blue-fronted Parrots *Amazona aestiva*: effects of nesting behaviour and cavity characteristics

Igor Berkunsky[1,*], **Luciano N. Segura**[2,3], **Rosana M. Aramburú**[3], **Román A. Ruggera**[4], **Walter S. Svagelj**[5] & **Juan C. Reboreda**[2]

In this study we analyse factors affecting nest survival in Blue-fronted Parrots *Amazona aestiva* breeding in the Chaco region of northern Argentina. We combined temporal and environmental variables in order to determine which best explain variation in overall nest survival and in predation dependent nest survival. We predicted that high and deep cavities, that are inaccessible to snakes and other predators, would have high daily survival rates. We compared the relative effects on nest survival of time of the breeding season, stage of the nesting cycle, and characteristics of the nest cavity. We modelled daily survival rate (DSR) for all observed nests, and daily survival rate for nests that had been predated (daily survival rate in relation to predation exclusively, DSR_p). Nest predation accounted for 50% of nest failures. DSR was on average 0.989, translating into an apparent hatching success of 0.39. DSR decreased with time of breeding and increased with nest age. DSR_p decreased with time of breeding and inclination of the nest cavity entrance hole and increased with height from the ground of the entrance hole. There was a quadratic effect of nest age on DSR_p, such that daily survival was highest during incubation, lowest at hatching and the early nestling stage, but increasing throughout the remainder of the nestling stage. This effect became more pronounced as the breeding season advanced. Year and observer effects did not affect the probability of survival. Temporal patterns and characteristics of the nest cavity explained most of the variation in nest survival in Blue-fronted Parrots, which highlights the relevance of including these covariates in future studies of nest survival in parrots, and has important management and conservation implications.

Key words: *Amazona aestiva*, breeding, MARK, nest survival, parrot, predation.

[1]Instituto Multidisciplinario sobre Ecosistemas y Desarrollo Sustentable, CONICET, Universidad Nacional del Centro de la Provincia de Buenos Aires, Paraje Arroyo Seco s/n, B7000GHG, Tandil, Argentina; [2]Departamento de Ecología, Genética y Evolución, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Pabellón II Ciudad Universitaria, C1428EGA Buenos Aires, Argentina; [3]División Zoología Vertebrados, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Paseo del Bosque s/n, B1900FWA La Plata, Argentina; [4]INECOA-UNJu, CONICET, Facultad de Ciencias Agrarias, Alberdi 47, San Salvador de Jujuy (4600), Jujuy, Argentina; [5]Instituto de Investigaciones Marinas y Costeras (IIMyC), Universidad Nacional de Mar del Plata, CONICET. Dean Funes 3250, Mar del Plata (B7602AYJ), Buenos Aires, Argentina;
*corresponding author (igorberkunsky@yahoo.com.ar)

Nest survival is the result of a wide range of processes, including intra- and interspecific interactions (i.e. competition, parasitism and predation), parental condition and behaviour, and weather (Newton 1998, Lima 2009). Temporal patterns, such as the date at which the nesting attempt started (i.e. time of breeding) or the stage of the nesting cycle (i.e. nest age), often influence nest survival (Grant *et al.* 2005, Lantz & Conway 2009,

Allen & Peters 2012). Many studies have also described correlations between nest site characteristics and nest survival (Martin & Roper 1988, Martin 1998, Colombell-Négrel & Kleindorfer 2009, Colwell *et al.* 2011).

Nest predation is probably an important factor affecting nest survival for lowland Amazon parrots *Amazona spp.*, but the effect of predation on nest survival has not been quantified (Rivera *et al.* 2013). Many studies on nest survival, mainly on passerines, where predation was the main cause of failure, show clear patterns of declining nest survival as the nesting season advances, and positive relationships between nest coverage and nest survival (Grant *et al.* 2005, Segura & Berkunsky 2012). Relationships between survival and nesting parameters are however more apparent in cases where there is a single cause of failure (Brown & Collopy 2008, Benson *et al.* 2010, Colwell *et al.* 2011), while in those studies where more than one cause of failure was significantly affecting nest survival, it was difficult to identify predictors of survival (Boulton *et al.* 2008, Kerns *et al.* 2010, Kozma & Kroll 2010). By grouping failure events together when trying to identify factors affecting nest survival, important predator-specific patterns are potentially obscured, which may lead to the conclusion that nest failures are random events (Benson *et al.* 2010). Yet, if cause-specific nest failures are predictable, this may have implications for the behaviour of individual birds and at the same time could help in the conservation and management of vulnerable species.

Cavity nest characteristics have been described for a large number of Neotropical parrot species, but only a small portion of these studies also reported nest survival. In recent years, the relationship between nest characteristics and nest survival at different stages of the nesting cycle has been studied more frequently (Ortiz-Catedral *et al.* 2013, Rivera *et al.* 2013, Berkunsky *et al.* 2014, Britt *et al.* 2014, Olah *et al.* 2014). However, only a small number of these studies found significant relationships between site-specific nest characteristics and nest survival (Koenig *et al.* 2007, Britt *et al.* 2014).

The Blue-fronted Parrot *Amazona aestiva* lives in subtropical forests and savannas of central South America (Caparroz *et al.* 2009). Like all Amazon parrots, it is a secondary cavity nester (Berkunsky & Reboreda 2009). Populations of this species are declining, mainly as a result of habitat transformation (e.g. deforestation and selective logging), and nestling harvesting for the pet trade (Berkunsky *et al.* 2012). Several previous studies described attributes of cavity use by Blue-fronted Amazons in Argentina and Brazil (Fernandes Seixas & De Miranda Mourão 2002, Berkunsky & Reboreda 2009, Berkunsky 2010), but only one study reported nest survival rates.

The objective of our work was to identify factors affecting nest survival in Blue-fronted Parrots. We combined a number of temporal and environmental variables in order to determine which best explain variation in the probability of nest survival and of nest predation. We explored if any of the cavity characteristics studied were related to nest survival, and we predicted that high and deep cavities (i.e. inaccessible for snakes and other predators) would have high daily survival rates.

METHODS

Study area

We conducted the study at the Loro Hablador Provincial Park (25°27'S, 61°51'W, 170 m ASL) and neighbouring areas, in the Chaco province, Argentina. The climate at the study site is dry-subtropical and mean temperatures vary between 27°C in January and 12.4°C in July. Average annual rainfall is near 700 mm and has a marked seasonality, with 80% of the rainfall occurring from November to March and an extended dry season from April to October (Bravo *et al.* 2010). The study area is a continuous dry forest dominated by White Quebracho *Aspidosperma quebracho-blanco* and Red Quebracho *Schinopsis lorentzii* (Tálamo & Caziani 2003).

Sampling procedure

Clutch size of the Blue-fronted Parrot is 2–3 eggs. On average, incubation lasts 28 days and nestlings fledge after 58 days (Berkunsky 2010). During egg-laying and incubation, females spent most of their time inside the nest or perched nearby, while males were never seen entering the nest cavity, although they often remained perched nearby (Figure 1; Berkunsky 2010).

We searched extensively for Blue-fronted Parrot nests from early October to late February during five consecutive breeding seasons (2002–2003 to 2006–2007). We found nests mainly by observing the behaviour of breeding pairs. After locating a potential nest (a tree with a cavity and parrot activity), we reached the entrance hole using climbing equipment.

We recorded the following nest site characteristics: tree species, diameter at breast height (dbh) of the tree, internal diameter at the bottom of the cavity depth of the cavity and thickness of the cavity wall (estimated as the difference between external and internal diameter).

Figure 1. (A) Incubating female Blue-fronted Parrot inside a tree cavity. (B) Brood of four nestlings between 26 and 32 days after hatching and (C) a brood of three nestlings just a few days before leaving the nest. Nestlings fledge on average when they are 58 days old.

We also took the following measurements of the nest entrance hole: height from the ground, minimum and maximum diameter, and inclination. We measured inclination as the angle between an axis perpendicular to the entrance hole area and the vertical line to the ground (see Berkunsky & Reboreda 2009). A value of 90° corresponded to an entrance hole with an axis perpendicular to the vertical plane. Smaller and greater values corresponded to holes that were oriented down or up, respectively. We assigned entrance hole inclination values to one of five categories: $-2 = 0°–22°$ (facing down), $-1 = 23°–67°$, $0 = 68°–112°$, $1 = 113°–157°$, and $2 = 158°–180°$ (facing up).

We monitored nests regularly until the nest failed or the nestlings fledged. On average, the interval between subsequent visits was 4.8 days (range 1–15 days). We considered a nest successful if it fledged at least one young. Fledging was confirmed by the following criteria: (1) we observed fully feathered young during the last visit to the nest, (2) the nest was undisturbed and in good condition at the time of fledging, and/or (3) we observed or heard fledglings nearby the nest

after the presumed time of fledging. We identified five different causes of nest loss: predation, adverse weather conditions, infertility of the eggs, death of the nestlings and abandonment due to an unknown cause. Nest loss due to predation was confirmed using one or more of the following criteria: (1) we observed broken eggshells, chick or adult remnants in or near to the basin of the nest tree, (2) we observed injuries in dead nestlings that would indicate attack by another animal, and/or (3) the nest was empty before the time of fledging. Nest loss due to adverse weather conditions included the fall of the nest-tree, breaking off of the branch with the nest cavity, or flooding of the cavity. To confirm nest loss due to infertility of the eggs, we inspected the egg content of unhatched eggs looking for a developed embryo visible with the naked eye (Birkhead *et al.* 2008). Nest loss due to death of the nestlings was previously reported in other Amazon species as 'dead-in-nest' (Koenig 2001), and this cause of failure was considered when all nestlings in a brood were found dead inside the cavity and without signs of starvation (their crops contained food) or predation (no teeth marks).

Statistical Analysis

We implemented Kaplan–Meier survival curves and we estimated hazard rates to describe the nest survival time (Lee & Wenyu Wang 2000). Kaplan–Meier (henceforth K–M) survival curves give information about when and how failures occur. Hazard rate is defined as the probability per day that a nest that has survived to the beginning of the day will fail during that day. Specifically, it is computed as the number of failures per day in the respective day, divided by the average number of surviving nests at the mid-point of the day. We built K–M curves with all nests that were found since egg-laying. In the case of nest failure, we estimated failure date as the mid-point between the last time the nest was seen active and the date when the failure was detected.

We estimated: (1) daily survival rate (DSR) for the complete dataset including all causes of nest failure ($n = 157$), and (2) daily survival rate in relation to predation only (DSR_p) for a reduced dataset ($n = 124$), from which we excluded all nests that failed due to causes other than predation. We estimated nesting success using the nest survival model in program MARK (White & Burnham 1999). We standardized the observation period for each nesting attempt by setting a maximum length of 85 d: 30 d for the egg-laying and incubation stages, assuming a clutch size of three eggs and incubation starting with the laying of the second egg, and 55 d for the fledging of the first young (Berkunsky 2010). Similarly, we assumed that the length of the breeding season was 117 days (from 20 October to 14 February) based on the period that nests were active during the five years of study. We used four temporal variables as covariates: year, time of breeding (i.e. date of the breeding season at which egg-laying started; 1 = 20 October), nest age (1 = day the first egg was laid), and day of visit, and nine nest cavity attributes (see above). We follow the approach described by Dinsmore & Dinsmore (2007) and standardized among years and did not use time of breeding adjusted for each year. We examined linear and quadratic effects of time of breeding and nest age and then used the best model to incorporate nest cavity characteristics. To evaluate possible effects of our visits on DSR, we included the day of the visit as a covariate. We also included temporal covariates following Rotella (2016), allowing DSR to vary following a trend in accordance with time of breeding and age of the nest. We adopted the default options of sin- (for constant survival models) or logit-link functions (for models including covariates) and second part variance estimation (Burnham & Anderson 2002). We obtained esti-

mates of nest survival for specific models using beta parameters and back transformation following Dinsmore *et al.* (2002) and Rotella (2016). Our model set was based on additive combinations of the aforementioned covariates.

We ranked all models according to second-order Akaike Information Criterion values corrected for small samples (AIC_c). We show summary tables with the null model $S(.)$ and models that rank higher than the null model. We kept models with combinations of variables only in those cases where the model with two or more combined variables ranked higher than models with a single variable (Rotella 2016). For example, if $S(date+age)$ ranked higher than $S(date)$ and $S(age)$, we would keep it, otherwise we removed it. The ΔAIC_c values indicate the magnitude of the difference in AIC_c values between each model and the best fitting model, and model likelihood assesses the strength of evidence for competing models. The AIC weight value (w_i) is the probability that model i is the best model, given the models considered. We calculated the proportion of nests that survived 85 days of exposure.

RESULTS

Nesting Success

We monitored 30, 30, 39, 37 and 21 nests during the breeding seasons 2002–2003 to 2006–2007, respectively, totalling 157 nests and 5888 exposure days. We found 52% of these nests ($n = 82$) before the start of egg-laying. In this subsample, 74% of the nests completed the incubation stage and 49% fledged at least
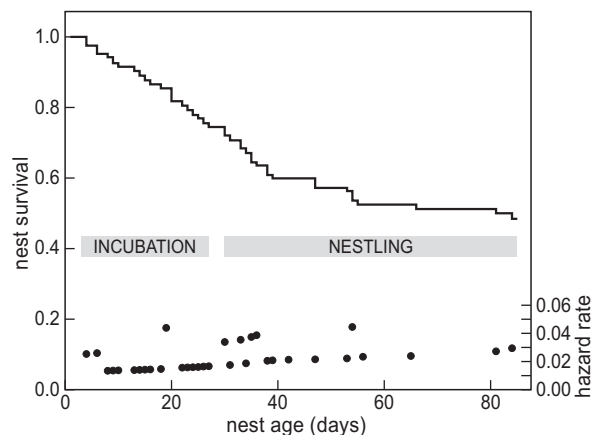
Figure 2. Kaplan–Meir survival curve for a subsample of 82 nests of Blue-fronted Amazon that were monitored since egg-laying in Chaco forests. Hazard rates (black dots) indicate a higher risk during the first days of nestling stage.

Figure 3. (A) Boa Constrictor *Boa constrictor occidentalis* visiting an active Blue-fronted Parrot nest cavity. (B) A Baron's Green Racer *Philodryas baroni* that was removed from a Blue-fronted Parrot nest cavity after partially ingesting a nestling.

one young. The number of surviving nests declined at a higher rate during incubation and the first days after hatching than during the rest of nestling period (Figure 2). Hazard rates were higher during the first days of the nestling stage.

Considering all nests found, 42% (66/157) failed. Main causes of nest failure were: predation ($n = 33$, 50% of the failures), dead nestlings ($n = 15$, 23%), abandonment because of unknown causes ($n = 8$, 12%), adverse weather ($n = 7$, 10%) and abandonment because of egg infertility ($n = 3$, 5%). Dead nestlings were found for ages ranging from 26 to 42 days (average 32.3 ± 5.0 (SD) days). None of the nests failed due to starvation.

Most direct and indirect evidence indicates that snakes were the main predators (Figure 3). Direct evidence included the capture of the following snakes at the time they were eating the nestlings: Rainbow Boa *Epicrates cenchria alvarezi* ($n = 1$), Boa Constrictor *Boa constrictor occidentalis* ($n = 2$), and Baron's Green Racer *Philodryas baroni* ($n = 2$). Indirect evidence of

snake predation was the disappearance of the entire nest content (i.e. we did not observe broken egg shells, chick feathers or adult remnants in or close to the nest). We also found a Spot-winged Falconet *Spiziapteryx circumcinctus* removing a 45-day-old nestling from its cavity.

Daily Nest Survival Rates

Daily nest survival rates ranged between 0.985 and 0.995 (Table 1), with an average value for the five study years of 0.989. Cumulative probability of nest survival during the 85 days of the nesting period was 0.39, so in 39% of the nests at least one nestling fledged, with a 95% confidence interval of 0.30–0.46. The best model explaining DSR incorporated the effects of time of breeding (date) and age of the nest (Table 2). Time of breeding showed a negative slope ($\beta_{date} = -0.044 \pm 0.009$ (SE)) indicating a decrease in survival as the breeding season advanced, while age of the nest showed a positive slope ($\beta_{age} = 0.046 \pm 0.008$) indicating an increase in survival as the nesting cycle advanced. Regarding daily nest survival in relation to predation exclusively (DSR_p), the overall 5-year survival rate was 0.994. The DSR_p model with the most support included the following covariates: time of breeding, age of the nest, inclination of the nest hole and height of the entrance hole from the ground (Table 3). This model had negative slopes for time of breeding ($\beta_{date} = -0.060 \pm 0.016$) and inclination of the entrance hole ($\beta_{inclination} = -0.687 \pm 0.243$) and a positive quadratic slope for nest age ($\beta_{age} = 0.0008 \pm 0.0002$) and height of the entrance hole ($\beta_{height} = 0.004 \pm 0.002$; Table 3 and Figure 4). There was no support for models containing year or visit day effects.

Table 1. Annual variation in daily nest survival rates (DSR) and cumulative seasonal nest survival of Blue-fronted Parrots *Amazona aestiva* at Loro Hablador Provincial Park, Argentina, estimated with the program MARK. Rows show estimated DSR for each year ($\pm$SE) and the average for the five years.

Year	DSR $\pm$ SE	95%-confidence interval	Cumulative probability of nest survival
2002–03	0.9898 ± 0.0038	0.979–0.995	41.8%
2003–04	0.9946 ± 0.0019	0.989–0.997	63.1%
2004–05	0.9880 ± 0.0030	0.980–0.993	35.8%
2005–06	0.9847 ± 0.0032	0.977–0.990	27.0%
2006–07	0.9884 ± 0.0035	0.979–0.994	37.1%
Average	0.9891 ± 0.0013	0.986–0.991	39.4%

Table 2. Results of AIC-based model selection identifying the main factors that influence daily survival rates (DSR) of Blue-fronted Parrot *Amazona aestiva* nests. Date = time of breeding, age = age of the nest, dbh = diameter at breast height of the nest-tree. Models are ranked according to the second-order Akaike Information Criterion corrected for small samples (AIC$_c$) values. K indicates the number of parameters of the model, ΔAIC$_c$ the difference between the AIC$_c$ value for the current model and the model with the lowest AIC$_c$, and w_i the model weight.

Model[*]	K	ΔAIC$_c$	w_i
S(date+age)	3	0.0	0.998
S(inclination)	2	14.1	0.001
S(age+age²)	3	17.2	0.000
S(dbh)	2	17.3	0.000
S(.)	1	17.5	0.000
S(year)	5	17.5	0.000
S(visit day)	2	19.5	0.000

[*]Survival of nests was modelled with the incorporation of covariates and compared with the null model of constant survival S (.).

Table 3. Results of AIC-based model selection identifying the main factors that influence daily survival rates of Blue-fronted Parrot *Amazona aestiva* nests, exclusively in relation to predation (DSR$_p$). Details on model selection and definitions of variables are provided in Table 2, plus height = height of the entrance of the cavity.

Model[*]	K	ΔAIC$_c$	w_i
S(date+age+age²+height+inclination)	6	0.00	0.662
S(date+age+age²+inclination)	5	1.77	0.274
S(date+age+age²+height)	5	5.85	0.035
S(date+age+age²)	4	6.55	0.025
S(inclination)	2	18.01	0.000
S(height)	2	22.25	0.000
S(.)	1	25.13	0.000
S(year)	5	26.43	0.000
S(visit day)	2	26.82	0.000

[*]

Figure 4. Predicted daily nest survival rates exclusively with respect to predation (DSR$_p$) of three hypothetical Blue-fronted Parrot nests starting at different times of the breeding season (early = 20 October, mid = 8 November and late = 23 November) as a function of the age of the nest (day 1 = start of laying). Lines represent DSR$_p$ estimated using beta parameters from the best-fit model (Tabel 3), incorporating age of the nest, date at which the nest started and average values of height and inclination of the entrance hole.

DISCUSSION

Time of breeding and nest age explained most variation in DSR in the Blue-fronted Parrot. Variation in DSR$_p$ was best explained by time of breeding, nest age and height and inclination of the entrance hole. Considering the overall results of the five breeding seasons, cumulative nest survival during the nesting phase was 39% and predation was the main cause of nest failure, accounting for 50% of the failures. As with other
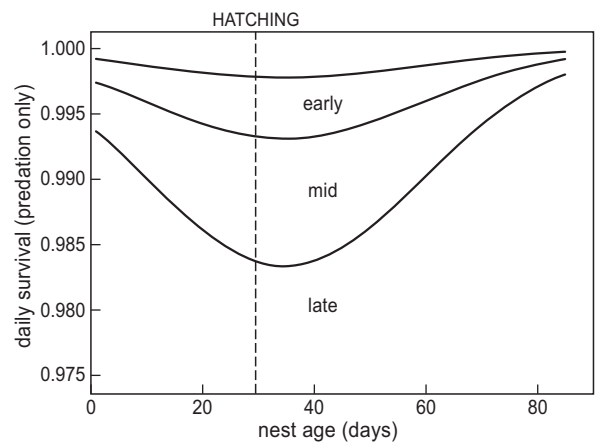
Amazon parrots (Koenig *et al.* 2007), most events of predation were attributable to snakes, particularly boas.

Nesting success of Blue-fronted Parrots in the Chaco region (39%) was lower than reported for the same species in a study conducted on a protected population in the Pantanal region of Brazil (average 61%, range 36%–72%, Fernandes Seixas & De Miranda Mourão 2002). In the latter study, DSR were estimated using the Mayfield method and therefore temporal factors and specific nest attributes that may have affected nest survival were not analysed. The high nest success found in Pantanal may be a consequence of lower predation pressure, as arboreal snakes are less common in savannahs like Pantanal than in subtropical dry forest (Leynaud & Bucher 1999) as in our study.

Nest survival rates reported for other species of Amazon parrots mostly did not differ considerably: 38% in Yellow-shouldered Amazon *Amazona barbadensis* of Margarita Island (Sanz & Rodríguez Ferraro 2006), 37% in Black-billed Amazon *Amazona agilis* (Koenig 2001), 42% in Bahama Amazon *Amazona leucocephala bahamensis* (Gnam & Rockwell 1991), 42% in *Amazona finschi* (Renton & Salinas-Melgoza 2004), 48% in Red-crowned Amazon *Amazona viridigenalis* and Red-lored Amazon *Amazona autumnalis* (Enkerlin-Hoeflich 1995) and 53% in Tucuman Amazon *Amazona tucumana* (Rivera *et al.* 2013). Studies on populations of Amazon parrots exposed to intense

poaching showed lower values of nesting success (i.e. 13% in Yellow-crowned Amazon *Amazona ochrocephala* in Panamá; Rodríguez Castillo & Eberhard 2006), while those conducted in populations with conservation management showed higher values of nesting success (i.e. 69 % in Puerto Rican Amazon *Amazona vittata*, Snyder *et al.* 1987).

In passerines, the decline in DSR with time of breeding has been generally attributed to an increase in the local abundance of predators as the breeding season progresses (Grant *et al.* 2005). Consistent with this interpretation, we observed a decline in both estimates of the daily survival rate, DSR and DSR_p, with time of breeding. Although we do not have information on changes of predator abundance over the breeding season, the activity of boas, which appears to be the main predator of Blue-fronted Parrot nests, increased as spring advanced and they were much more frequently observed at our study site during November and December (Kacoliris *et al.* 2006, Berkunsky *et al.* 2011). The seasonal pattern of nest failure could also be partially explained by the increase in the frequency of heavy storms as the breeding season advances (Bravo *et al.* 2010). Heavy storms often bring down trees and flood cavities.

We also observed that DSR_p had the lowest value at the time of hatching and that this temporal pattern was more marked as the breeding season progressed. The pattern of a drop in nest survival immediately after hatching and then an increase until fledging has been observed in several passerines (Grant *et al.* 2005, Davis *et al.* 2006, Grant & Shaffer 2012) and it is generally attributed to an increase in activity levels of the young and parents at the nest site, which may attract predators (Grant *et al.* 2005). In Blue-fronted Parrots, the female performs all the incubation and during this period the male feeds the female at the nest entrance (Berkunsky 2010). During the first week after hatching, the male feeds both the female and the chicks. After that period, both sexes share nestling provisioning. These changes in parental behaviour at the time of hatching (or shortly after) could lead to detection by predators. In addition, the more pronounced drop in DSR_p at the time of hatching as the breeding season advances provides indirect evidence for the decline in DSR with time of breeding mainly being the result of predation.

Some of the most frequently discussed architectural attributes of nest cavities are the dimensions and exposure of the entrance-hole (Rendel & Robertson 1994, Wiebe 2001, Politi *et al.* 2009, Cockle *et al.* 2011). Secondary cavity-nesters usually select deep cavities far above the ground in relatively isolated trees with good visibility, perhaps reducing their risk of predation (Cockle *et al.* 2011). In our study, most of the architectural attributes did not explain survival rates. The only two cavity attributes that explained variation in survival in relation to predation exclusively were the inclination of the entrance hole and its height from the ground. This could be related to the difficulty that snakes may have in climbing nests that are high up in trees and with entrance holes facing the ground. Because DSR_p was well correlated with cavity height and inclination of the entrance hole, either characteristic should be a reasonable indicator of nest-site quality and could serve as a cue for nest-site selection by Blue-fronted Parrots. Yet they frequently used cavities that could be classified as 'poor quality' nest-sites, given their height and inclination of the entrance hole, which raises the question of whether 'good quality' nest-sites are limited at our study site.

We provided detailed estimates of nest survival that could be used in current and future management plans for the Blue-fronted Amazon in Chaco woodlands. According to the concept of sustainable wild parrot harvesting, removal quotas are established based on the number of parrots that usually die from natural causes, such as brood reduction and/or predation (Beissinger & Bucher 1992). In the absence of better information, the National Fauna Authority of Argentina is estimating harvest quotas based on data of a non-harvested wild Turquoise-fronted Amazon population on savannahs of Brazil as reported by the same Agency (Fernandes Seixas & de Miranda Mourao 2002, Rabinovich 2004). It would also be important to consider that any harvesting will be additional to natural nest failure, and hence increase the overall failure rate. We hope our estimates and models help authorities to review and modify current quotas.

To summarize, our results show that temporal patterns and characteristics of the nest cavity together explain most variation in nest survival in Blue-fronted Parrots and highlight the relevance of including these covariates in future studies of nest survival in parrots. We provided detailed estimates of nest survival that could be used in current and future management plans to conserve the Blue-fronted Amazon in Chaco woodlands.

ACKNOWLEDGEMENTS

REFERENCES

Allen M.C. & Peters K.A. 2012. Nest survival, phenology, and nest-site characteristics of Common Nighthawks in a New Jersey Pine Barrens grassland. Wilson J. Ornithol. 124: 113–118.

Beissinger, S.R. & Bucher E.H. 1992. Can parrots be conserved through sustainable harvesting? BioScience 42: 164–173.

Benson T.J., Brown J.D. & Bednarz J.C. 2010. Identifying predators clarifies predictors of nest success in a temperate passerine. J. Anim. Ecol. 79: 225–234.

Berkunsky I. 2010. Ecología reproductiva del Loro Hablador (*Amazona aestiva*) en el Chaco Argentino. Tesis doctoral. Universidad Nacional de La Plata, La Plata, Buenos Aires, Argentina.

Berkunsky I. & Reboreda J.C. 2009. Nest-site fidelity and cavity reoccupation by Blue-fronted Parrots *Amazona aestiva* in the dry Chaco of Argentina. Ibis 151: 145–150.

Berkunsky I., Kacoliris F.P., Faegre S.I., Ruggera R.A., Carrera J. & Aramburú R.M. 2011. Nest predation by arboreal snakes on cavity-nesting birds in dry Chaco woodlands. Ornitol. Neotrop. 22: 459–464

Berkunsky I., Ruggera, R., Aramburú R.M. & Reboreda J.C. 2012. Principales amenazas para la conservación del Loro Hablador (*Amazona aestiva*) para la región del Impenetrable, Argentina. Hornero 27: 39–49.

Berkunsky I., Daniele G., Kacoliris F.P., Diaz, J.A., Aramburú R.M. & Gilardi J.D. 2014. Reproductive parameters in the critically endangered Blue-throated Macaw: limits to the recovery of a parrot under intensive management. Plos ONE 9(6): e99941.

Birkhead T.R., Hall J., Schut E. & Hemmings N. 2008. Unhatched eggs: methods for discriminating between infertility and early embryo mortality. Ibis 150: 508–517.

Boulton R.L., Richard Y. & Armstrong D.P. 2008. Influence of food availability, predator density and forest fragmentation on nest survival of New Zealand robins. Biol. Conserv. 141: 580–589.

Bravo S., Kunst C., Grau R. & Araoz E. 2010. Fire-rainfall relationships in Argentine Chaco savannas. J. Arid Environ. 74: 1319–1323

Britt C.R., García Anleu R. & Desmond M.J. 2014. Nest survival of a long-lived psittacid: Scarlet Macaws (*Ara macao cyanoptera*) in the Maya Biosphere Reserve of Guatemala and Chiquibul Forest of Belize. Condor 116: 265–276.

Brown J.L. & Collopy M.W. 2008. Nest-site characteristics affect daily nest-survival rates of Northern Aplomado Falcons (*Falco femoralis septentrionalis*). Auk 125: 105–112.

Burnham K.P. & Anderson D.R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York.

Caparroz R., Fernades-Seixas G.H., Berkunsky I. & García-Collevatti R. 2009. The role of demography and climatic events in shaping the phylogeography of *Amazona aestiva* (Psittaciformes, Aves) and definition of management units for conservation. Divers. Distrib. 15: 459–468.

Cockle K., Martin K. & Wiebe K.L. 2011. Selection of nest trees by cavity-nesting birds in the Neotropical Atlantic forest. Biotropica 43: 228–236.

Colombell-Négrel D. & Kleindorfer S. 2009. Nest height, nest concealment, and predator type predict nest predation in superb fairy-wrens (*Malurus cyaneus*). Ecol. Res. 24: 921–928.

Colwell M.A., Meyer J.J., Hardy M.A., Mcallister S.E., Transou A.N., Levalley R.R. & Dinsmore S.J. 2011. Western Snowy Plovers *Charadrius alexandrinus nivosus* select nesting substrates that enhance egg crypsis and improve nest survival. Ibis 153: 303–311.

Davis S.K., Brigham R.M., Shaffer T.L. & James P.C. 2006. Mixed-grass prairie passerines exhibit weak and variable responses to patch size. Auk 123: 807–821.

Dinsmore S.J. & Dinsmore J.J. 2007. Modelling avian nest survival in program MARK. Stud. Avian Biol. 34: 73–83.

Dinsmore S.J., White G. C. & Knopf F.L. 2002. Advanced techniques for modeling avian nest survival. Ecology 83: 3476–3488.

Enkerlin-Hoeflich E. 1995. Comparative ecology and reproductive biology of three species of Amazona Parrots in North-eastern Mexico. Thesis, Texas A&M University, Texas, USA.

Fernandes Seixas G.H. & De Miranda Mourão G. 2002. Nesting success and hatching survival of the Blue-fronted Amazon (*Amazona aestiva*) in the Pantanal of Mato Grosso do Sul, Brazil. J. Field Ornithol. 73: 399–409.

Gnam R. & Rockwell R.F. 1991. Reproductive potential and output of the Bahamas parrot *Amazona leucocephala bahamensis*. Ibis 133: 400–405.

Grant T.A., Shaffer T.L., Madden E.M. & Pietz P.J. 2005. Time-specific variation in passerine nest survival: New insights into old questions. Auk 122: 661–672.

Grant T.A. & Shaffer T.L. 2012. Time-specific patterns of nest survival for ducks and passerines breeding in North Dakota. Auk 129: 319–328.

Ibáñez-Álamo J.D., Magrath R.D., Oteyza J.C., Chalfoun A.D., Haff T.M., Schmidt K.A., Thomson R.L. & Martin T.E. 2015. Nest predation research: recent findings and future perspectives. J. Ornithol. 156: S247–S262.

Kacoliris F.P., Berkunsky I. & Williams J. 2006. Herpetofauna of the Argentinean impenetrable Great Chaco. Phyllomedusa 5: 149–157.

Kerns C.K., Ryan M.R., Murphy R.K., Thompson F.R. & Rubin C.S. 2010. Factors affecting songbird nest survival in northern mixed-grass prairie. J. Wildl. Manage. 74: 257–264.

Koenig S.E. 2001. The breeding biology of Black-billed Parrot *Amazona agilis* and Yellow-billed Parrot *Amazona collaria* in Cockpit Country, Jamaica. Bird Conserv. Int. 11: 205–225.

Koenig S.E., Wunderle J. & Enkerlin-Hoeflich E.C. 2007. Vines and canopy contact: A route for snake predation on parrot nests. Bird Conserv. Int. 17: 79–91.

Kozma J.M. & Kroll J. 2010. Nest survival of Western Bluebirds

using tree cavities in managed Ponderosa Pine forests of Central Washington. Condor 112: 87–95.

Lantz S.J. & Conway C.J. 2009. Factors affecting daily nest survival of Burrowing Owls within Black-Tailed Prairie Dog colonies. J. Wildl. Manage. 73: 232–241.

Lee E.T. & Wenyu Wang J. 2000. Statistical methods for survival data analysis. John Wiley & Son, New Jersey.

Leynaud G.C. & Bucher E.H. 1999. La fauna de serpientes del Chaco sudamericano: Diversidad, distribución geográfica y estado de conservación. Miscelánea 98. Academia Nacional de Ciencias, Córdoba, Argentina.

Lima S.L. 2009. Predators and the breeding bird: behavioral and reproductive flexibility under the risk of predation. Biol. Rev. Camb. Philos. Soc. 84: 485–513.

Martin T.E. 1998. Are microhabitat preferences of coexisting species under selection and adaptive? Ecology 79: 656–670.

Martin T.E. & Roper T.E. 1988. Nest predation and nest site selection of a western population of the Hermit Thrush. Condor 90: 51–57.

Newton I. 1998. Population limitation in birds. Academic Press, London.

Olah G., Vigo G., Heinsohn R. & Brightsmith D.J. 2014. Nest site selection and efficacy of artificial nests for breeding success of Scarlet Macaws *Ara macao macao* in lowland Peru. J. Nat. Conserv. 22: 176–185.

Ortiz-Catedral L., Hauber M.E. & Brunton D.H. 2013. Growth and survival of nestlings in a population of red-crowned parakeets (*Cyanoramphus novaezelandiae*) free of introduced mammalian nest predators on Tiritiri Matangi Island, New Zealand. New Zeal. J. Ecol. 37: 370–378.

Politi N., Hunter Jr. M. & Rivera L. 2009. Nest selection by cavity-nesting birds in subtropical montane forests of the Andes: implications for sustainable forest management. Biotropica 41: 354–360.

Rabinovich J.E. 2004. Modelling the sustainable use of the Blue-fronted Parrot (*Amazona aestiva*) in the Dry Chaco Region of Argentina. Wildlife Service Technical Report, Secretary of the Environment and Sustainable Development of Argentina, Buenos Aires.

Rendell W.B. & Robertson R.J. 1994. Cavity-entrance orientation and nest-site use by secondary hole-nesting birds. J. Field Ornithol. 65: 27–35.

Renton K. & Salinas-Melgoza A. 2004. Climatic variability, nest predation, and reproductive output of Lila-crowned Parrots (*Amazona finschi*) in tropical dry forest of western Mexico. Auk 121: 1214–1225

Rivera L., Politi N., Bucher E. & Pidgeon A. 2013. Nesting success and productivity of Tucuman Parrots (*Amazona tucumana*) in high-altitude forests of Argentina: do they differ from lowland Amazona parrots? Emu 114: 41–49.

Rodríguez Castillo A.M. & Eberhard J.R. 2006. Reproductive behavior of the Yellow-crowned parrot (*Amazona ochrocephala*) in Western Panama. Wilson J. Ornithol. 118: 225–236.

Rotella J. 2016. Nest survival models. In: Cooch E. & White G. (eds) Program MARK: A gentle introduction, 14th Edition. www.phidot.org/software/mark/docs/book

Sanz V. & Rodríguez-Ferraro A. 2006. Reproductive parameters and productivity of the Yellow-shouldered Parrot on Margarita Island, Venezuela: A long-term study. Condor 108: 178–192.

Segura L.N. & Berkunsky I. 2012. Supervivencia de nidos del Cardenal común (*Paroaria coronata*) en un hábitat modificado en Argentina. Ornitol. Neotrop. 23: 489–498.

Snyder N.F.R., Wiley J.W. & Kepler C.B. 1987. The Parrots of Luquillo. Natural history and conservation of the Puerto Rican Parrot. Western Foundation of Vertebrate Zoology, Los Angeles, CA.

Tálamo A. & Caziani S.M. 2003. Variation in woody vegetation among sites with different disturbance histories in the Argentine Chaco. Forest Ecol. Manag. 184: 79–92.

White G.C. & Burnham K.P. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46: 120–139.

Wiebe K.L. 2001. Microclimate of tree cavity nests: is it important for reproductive success in Northern Flickers? Auk 118: 412–421.

SAMENVATTING

Van vogels in (sub)tropische ecosystemen is weinig bekend over de oorzaken van nestmislukking en de eigenschappen van het nest die op het mislukken van invloed zijn. In dit onderzoek zijn de factoren onderzocht die van invloed zijn op de overlevings-kansen van de nestinhoud van de Blauwvoorhoofdamazone *Amazona aestiva*, een amazonepapegaai die voorkomt in de subtropische bossen en savannes van centraal Zuid-Amerika. Deze papegaaiensoort wordt bedreigd door habitatfragmentatie en de illegale handel in dieren. Blauwvoorhoofdamazones zijn holenbroeders die gebruikmaken van bestaande boomholtes. De onderzoekers maakten in hun analyses onderscheid tussen nesten die mislukten als gevolg van predatie en nesten die door andere oorzaken mislukten. Het onderzoek vond plaats in het aaneengesloten droog subtropisch bos van het Loro Hablador Provinciale Park in Argentinië. In dit gebied lokaliseerden de onderzoekers tijdens vijf broedseizoenen (2002/03–2006/07) in totaal 157 nesten. Door de nestplaatsen regelmatig te bezoeken konden de lotgevallen van de nesten op de voet worden gevolgd. Voor elk nest werd vastgesteld of de jongen succesvol uitvlogen of niet. Van de 157 nesten mislukten er 66 (42%). De rest had minimaal één uitgevlogen jong. De overle-vingskans van de nestinhouden nam af naarmate later in het seizoen werd begonnen met broeden en het broedproces verder was voortgeschreden. Een belangrijke oorzaak van het mis-lukken van nesten was predatie (33 nesten, 50% van de mis-lukte nesten). De kans op predatie nam toe naarmate de vogels later in het seizoen waren gaan broeden en de nestingang minder steil omhoog liep. De kans nam echter af naarmate het nest hoger in de boom zat. De dagelijkse kans op nestmisluk-king ten gevolge van predatie was het kleinst tijdens de broed-periode en het grootst tijdens het uitkomen van de jongen en kort erna. Naarmate de jongen ouder werden, nam de overle-vingskans weer toe. De onderzoekers concludeerden dat het belangrijk is om de nesteigenschappen en tijdsgebonden varia-belen die de overlevingskans van de nestinhoud van papegaaien bepalen mee te nemen bij toekomstig onderzoek aan deze vogels alsmede bij het opstellen van beschermingsplannen voor deze soorten.